

## Costs of large communal clutches for male and female Greater Rheas *Rhea americana*

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The breeding system of the Greater Rhea *Rhea americana* is almost unique among birds as it combines harem polygyny and sequential polyandry, with communal egg-laying and uniparental male care. In this species, large communal clutches (more than 30 eggs) are rare and have a lower hatching success than smaller clutches. Here we analyse the proximate causes of hatching failures and the costs of large communal clutches (and therefore the costs of extensive polygyny) for males and females. We evaluated if length of the nesting period, egg viability, egg losses during incubation and male parental activity at the nest were affected by clutch size. We also evaluated if chicks hatched from large clutches have a lower survival during the first 2 months after hatching. Large clutches had longer nesting period and lower hatching success, mainly as a result of bacterial contamination of the eggs and increased hatching asynchrony. In addition, large clutches tended to lose more eggs as a result of accidental breakage or predation. Male activity at the nest and chick survival were not related to clutch size. Low hatching success, nest predation risk and energetic costs associated with large clutches penalize females that join large harems and males that accept additional eggs into the nest.

The adaptive significance of clutch size in birds has been widely debated and remains controversial (e.g. Partridge & Harvey 1988, Godfray *et al.* 1991). Although parent fitness might increase almost linearly with the number of eggs laid in the clutch, there are several costs associated with large clutches that make this relationship non-linear. Lack (1947) suggested that clutch size in some precocial species has an upper limit set by the incubation capacity of the parent ('the incubation capacity hypothesis'). According to this hypothesis, large clutches have lower hatchability mainly as a result of the inability of parents to incubate and/or protect the eggs efficiently (Yogev *et al.* 1996, Arnold 1999). Large clutches could also increase the risk of nest predation as a result of making the nest more attractive to predators, or increasing the traffic of the parent to and from the nest, which may facilitate its detection by predators (Lack 1947, Perrins 1977, Arnold 1999). Several studies have found that enlargement of

clutches of precocial birds resulted in increased egg losses and higher rates of nest desertion (e.g. Armstrong & Robertson 1988, Sandercock 1997). Thus, high rates of nest predation may select for reduced clutch size. In addition, parental behaviour at the nest can be affected in large clutches. Large clutches can be energetically more costly for the incubating parent and this may result in an increase in the proportion of time the parent spends foraging, thus reducing the proportion of time it spends incubating (Thomson *et al.* 1998). The 'incubation capacity hypothesis' can be extended to include parental behaviour after chick hatching. Safriel (1975) suggested that clutch size in nidicolous species could be limited by the ability of the parent to cover and protect broods ('the parental-care hypothesis'; Safriel 1975, Winkler & Walters 1983, Lessels 1986, Dzus & Clark 1997, Wallander & Andersson 2002, Larsen *et al.* 2003). Chicks hatched from large clutches could have a reduced survival after leaving the nest, and also affect parental physical condition (Dzus & Clark 1997, Nol *et al.* 1997). Furthermore, large clutches may result in parents spending more time in

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laying and incubation (Coleman & Whittall 1988, Sandercock 1997, Reid *et al.* 2000, Larsen *et al.* 2003), thus increasing both the energetic costs associated with these stages (Winkler & Walters 1983, Godfray *et al.* 1991, Tinbergen & Williams 2002) and hatching asynchrony (Sandercock 1997). Besides, if incubation of large clutches is energetically more costly, parents may have a higher probability of deserting the nest (Delehanty & Oring 1993).

The Greater Rhea *Rhea americana* is a large, precocial, flightless bird that inhabits grasslands and open areas of the Southern Neotropical Region. Rheas differ from most birds as females lay eggs communally and males incubate the eggs and care for the chicks without the assistance of females (Bruning 1974). The mating system of Greater Rheas combines harem polygyny and sequential polyandry. Females lay eggs every 48–72 h for 10–12 days in a single communal nest attended by the male (Bruning 1974, Fernández & Reboreda 1998). After the laying of 3–5 eggs, the male sits in the nest. Females then start laying eggs at the periphery of the nest and the male rolls them into the nest with his bill. Once females complete laying for one male, they can start laying for another male (Muñiz 1885; Astley 1907, Van Heyst 1950, Bruning 1974). Incubation lasts 36–40 days. Although incubation starts during laying, chicks hatch relatively synchronously, within 24–36 h (Bruning 1974). Thus, female parental investment in Greater Rheas is restricted to the production of eggs, whereas males perform all incubation and care of the chicks after hatching (Muñiz 1885; Adams 1908, Bruning 1974, Fernández & Reboreda 1998).

In a previous study, we found that clutch size in Greater Rheas varied between 13 and 56 eggs and that large clutches (i.e. clutches with more than 30 eggs) were uncommon and had a lower hatching success than clutches of fewer than 30 eggs (Fernández & Reboreda 1998). In this work, we analyse the proximate causes of hatching failures in large clutches and the costs for nesting males and females associated with large clutches. We specifically analyse if the increase of clutch size is associated with: (1) an increase in length of the nesting period, hatching asynchrony and hatching failures; (2) higher egg losses and nest desertion rates (predation hypothesis); (3) an increase in off-nest bouts of the male during incubation; and (4) a decrease of chick survival after hatching. Additionally, we would expect that the frequencies of clutch sizes were positively associated with their hatching success and therefore with the

number of chicks produced. Also, in order to assess if the incubating male exerts some control over the number of eggs in its nest, we evaluated his response to experimentally offered foreign eggs. If males control clutch size, we would expect them not to accept eggs once incubation has started.

## METHODS

The study was conducted in two adjacent cattle ranches situated 20–40 km southwest of General Lavalle, Buenos Aires province, Argentina (36°25'S, 56°56'W), during the breeding seasons (September–December) of 1992–95. The study area comprises grassland with shallow ponds interspersed, it covers an area of approximately 4300 ha, and it supports a Rhea population of roughly 400 individuals.

During each breeding season, we searched for nests intensively over the entire study site. Nests were found mainly by chance while driving slowly across the landscape. Nests were visited from 09:00 to 17:00 h at 1- to 4-day intervals. We marked each egg with an indelible ink pen the first day we found it. On each visit we registered the position of the eggs in the nest, and whether there was any missing egg. Nest visits lasted less than 20 min. The majority of the nests were unaffected by our visits and manipulations. During our study only four nests (< 4%) were deserted after we visited them. These nests were not included in the analyses.

We dated the start of the laying either directly (we knew the date of laying of the first egg) or indirectly by backdating using the colour of the eggs (they are light yellow when laid but become white in approximately 5 days). The length of the laying period was estimated as the time elapsed between the laying of the first egg and the laying of the last egg not to be followed by a laying interval greater than 24 h. We used this criterion because in some cases (less than 10% of nests) a few eggs were laid during mid or late incubation (20–35 days after the laying of the first egg). We estimated the length of the nesting period as the time elapsed since the laying of the first egg until the male left the nest with the chicks (it includes laying, incubation and hatching periods). We use the term clutch size to refer to the total number of eggs laid in a nest. As these eggs are laid by several females, the term clutch size is used from the male's point of view.

Nesting success was calculated as the number of nests where chicks hatched divided by the number of nesting attempts. Egg success was calculated as

the number of chicks hatched in a nest divided by the number of eggs laid in that nest, and hatching success (or hatchability; Koenig 1982) was calculated as the number of chicks hatched in a nest divided by the number of eggs before hatching in that nest (number of eggs laid minus egg losses during incubation).

The causes of hatching failure were determined by dissecting the eggs that remained in the nest after hatching. Eggs that did not hatch were classified as: eggs with incomplete development, when some degree of embryo development was noted; undeveloped, when no visible evidence of embryo development was detected; and infected, when eggs were rotten as a result of bacterial contamination. In addition, there were cases in which the eggs had an almost complete development (i.e. the chick had the yolk sac reabsorbed) and did not hatch because the male left the nest after the hatching of the majority of the chicks.

The rate of egg losses was estimated on the basis of exposure time. A daily egg mortality rate (DEMUR) was calculated as the number of eggs lost divided by the days the nest was under observation (Mayfield 1975). In order to avoid bias when no eggs were lost, we modified the estimator using:  $\text{egg losses/day} = (0.5 + \text{number of eggs lost})/\text{nest-days}$ . Egg losses due to other causes not relevant for this study (e.g. cattle ranching or flooding) were excluded from our analysis.

We measured the incubation temperatures of the eggs in nine active nests with clutch sizes that varied between 15 and 44 eggs (mean  $\pm$  se:  $22.4 \pm 2.8$  eggs). In order to minimize the risk of nest desertion by the incubating male, we measured temperatures during mid or late incubation (20–40 days after the laying of the first egg). We measured egg temperatures at the centre of each nest using a miniature temperature logger (Tinytalk-temp, Orion Components Ltd). The thermistor of the temperature logger was introduced in a fresh natural orphan egg (unattended eggs laid far from active nests; see Navarro *et al.* 1998) through a small hole in the equatorial plane and fixed to the eggshell with epoxy adhesive. The egg was attached with a wire to the centre of the nest in a natural position and the data logger was buried under the nest. The data logger automatically recorded the temperature at 3.8- or 6-min intervals over 4 or 6 days, respectively. None of these nests was deserted after our manipulation.

We used the variation in egg temperature to determine when the male left the nest (Hainsworth *et al.* 1998, Flint & Grand 1999). We assumed that the male left the nest when the difference in egg temperature was  $|T(t) - T(t-1)| > 1^\circ\text{C}$ , where  $T(t)$  and

$T(t-1)$  are egg temperatures at a time interval of 15 min when data loggers were set at 3.8-min intervals or 18 min when they were set at 6-min intervals (Fernández & Reboreda 2003). We considered that the male was outside the nest from the time at which the difference between  $T(t)$  and  $T(t-1)$  was negative until the time it was positive (i.e. the male resumed incubation). Although the sun can heat eggs when the male is absent (particularly at midday), unattended eggs never reached temperatures above  $30^\circ\text{C}$  (Fernández & Reboreda 2003). Therefore, it was possible for us to discriminate between an increase in temperature produced by the sun and one produced by males when they resume incubation.

Chick survival was estimated through the resighting of the group of male and chicks during the 2 months following nest departure. Although males were unmarked, we could recognize most groups of males with chicks because during this period they remained near the nest-site.

### Egg addition experiment

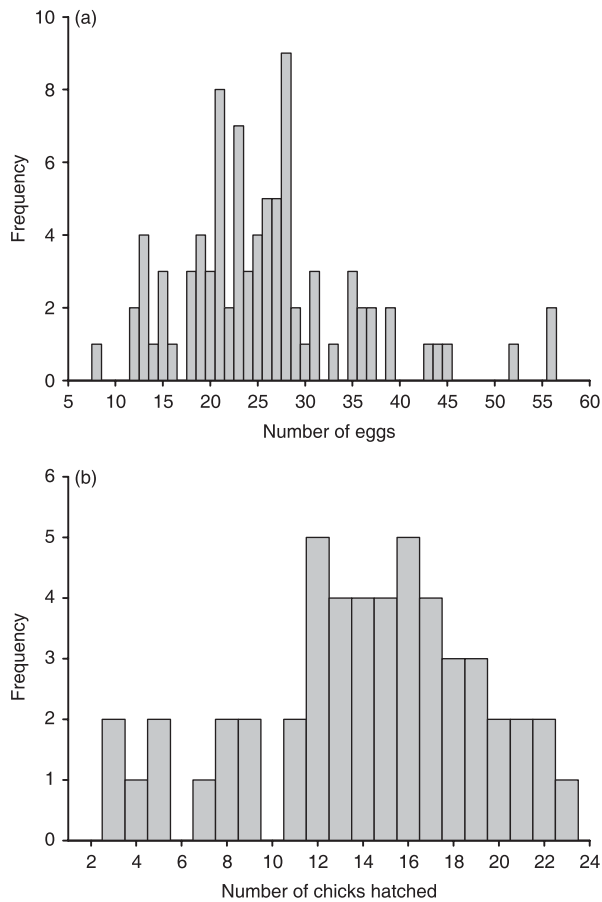
In order to test if the incubating male has some degree of control over the size of the clutch, we performed experiments of egg addition in 16 active nests. For these experiments, we used recently laid eggs taken from early deserted nests or orphan eggs found in the study area. In each nest we placed a single egg 1.5 m from the border of the nest. The experiment was performed during mid incubation (> 20 days after the laying of the first egg) and in nests with a clutch size of 25–30 eggs. These nests were monitored the following day when possible. We considered that the experimental egg was accepted if it was in the nest when we next visited the nests. We also tested if the egg addition affected nest or egg survival.

Data below are presented as mean  $\pm$  se. When possible we used parametric statistical tests. To meet parametric assumptions, we transformed rates and proportions using the square root and arcsine of the squared root of the value, respectively. Otherwise, we used non-parametric tests. All significance levels are for two-tailed tests.

## RESULTS

### Egg success, and hatching success

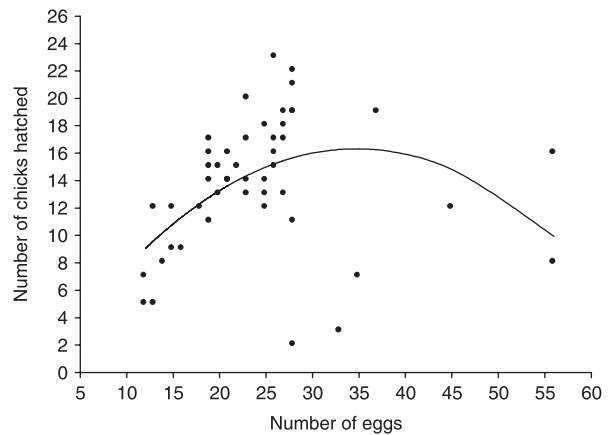
The modal number of eggs laid was 28 (range 8–56,  $n = 87$ ; Fig. 1a). We did not find annual or seasonal



**Figure 1.** (a) Frequency distribution of clutch sizes observed in nests of Greater Rheas that completed egg-laying for the 1992–96 breeding seasons. (b) Frequency distribution of number of chicks hatched from Greater Rhea successful nests in the same period. Data correspond to 87 nests that completed laying (a) and 51 nests that hatched chicks (b).

variation in the number of eggs laid (two-way ANOVA,  $F_{3,68} = 1.38$ ,  $P = 0.25$  for year;  $F_{2,68} = 0.57$ ,  $P = 0.57$  for month;  $F_{6,68} = 1.16$ ,  $P = 0.34$  for year  $\times$  month term). The number of chicks hatched did not differ among years or hatching date within the breeding season (two-way ANOVA,  $F_{3,45} = 0.16$ ,  $P = 0.92$  for year;  $F_{2,45} = 0.69$ ,  $P = 0.50$  for hatching date;  $F_{6,45} = 1.33$ ,  $P = 0.27$  for hatching date  $\times$  year term).

The number of chicks hatched per nest was  $13.8 \pm 0.74$  (mode = 13, range 1–23,  $n = 51$ ; Fig. 1b). Seventy-eight per cent ( $78.4 \pm 2.35$ ) of the eggs that were at the nest before hatching had some degree of embryo development but only 64.2% ( $\pm 2.76$ ) hatched. The number of chicks hatched increased almost linearly with clutch size, but in nests with



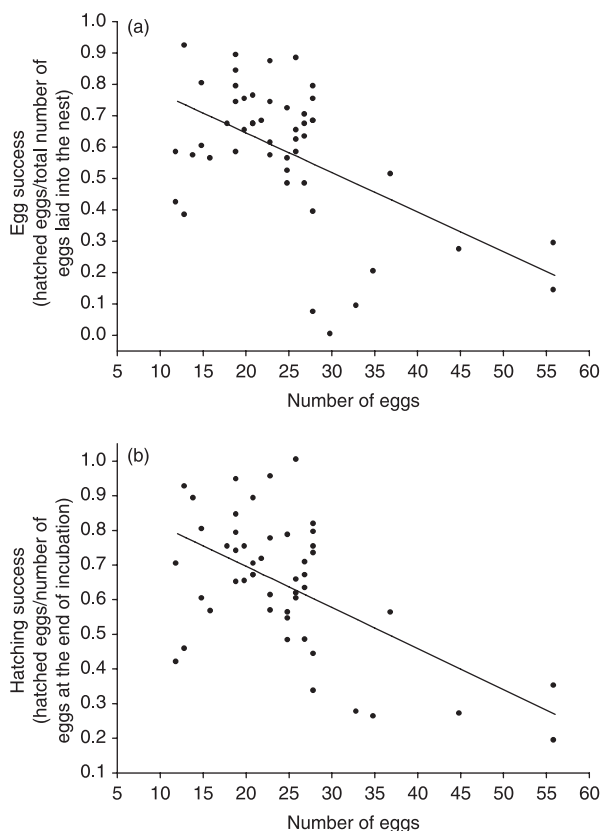
**Figure 2.** Number of chicks hatched as a function of clutch size. Data from 49 successful nests.

more than 30 eggs this relationship was reversed (regression ANOVA,  $F_{2,46} = 528$ ,  $P < 0.0001$ ; Fig. 2). Egg success decreased with the number of eggs in the nest (regression ANOVA,  $F_{1,50} = 13.1$ ,  $P < 0.001$ ; Fig. 3a). In addition, hatchability of eggs that were present in the nest at the end of incubation decreased as clutch size increased (regression ANOVA,  $F_{1,47} = 14.2$ ,  $P < 0.001$ ; Fig. 3b).

Hatching failures in large clutches were the consequence of an increase in the number of infected eggs (regression ANOVA,  $F_{1,44} = 3.94$ ,  $P < 0.001$ ; Fig. 4) and eggs with incomplete embryo development (regression ANOVA,  $F_{1,44} = 2.48$ ,  $P = 0.02$ ; Fig. 4). The number of eggs without embryo development did not vary with clutch size ( $F_{1,44} = 0.07$ ,  $P = 0.94$ ). When we excluded from our analysis nests with clutch sizes of over 30 eggs, the relationship between clutch size and number of eggs that did not hatch by incomplete embryo development was not significant ( $F_{1,43} = 1.34$ ,  $P = 0.19$ ). However, the relationship between clutch size and number of eggs that did not hatch due to bacterial contamination was still close to significance ( $F_{1,41} = 2.76$ ,  $P = 0.08$ ).

### Nest desertion and egg losses

Sixty-seven per cent (114/170 nests) of nesting attempts failed during laying and incubation. The fate of the nests that saw the completion of egg-laying was not predicted by either the number of eggs laid (standard logistic regression, Wald test = 0.06,  $P = 0.82$ ) or by the day of the breeding season (Wald test = 4.18,  $P = 0.65$ ). The number of eggs in nests that were deserted or predated was  $26.6 \pm 1.72$



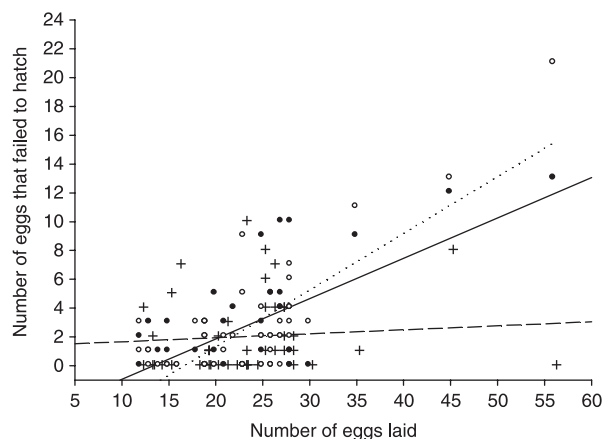
**Figure 3.** (a) Proportion of laid eggs that hatched (egg success), and (b) proportion of eggs present in the nests at the end of incubation that hatched (hatching success) as a function of clutch size.

( $n = 28$ ) whereas the number of eggs in nests that produced chicks was  $25.06 \pm 1.26$  ( $n = 50$ ).

In nests that survived until hatching,  $9.42 \pm 0.31\%$  of eggs were lost during the incubation (range 0–78.6%,  $n = 50$  nests). The number of eggs lost during incubation tended to increase with clutch size, although the association was not significant (Spearman rank correlation,  $n = 49$ ,  $Rho = 0.25$ ,  $t = 1.76$ ,  $P = 0.08$ ; for this analysis we excluded one nest where most eggs were lost as a result of egg infection and breakage).

### Length of nesting period, parental activity at the nest and chick survival

The length of the nesting period increased with the size of the clutch (regression ANOVA,  $F_{1,20} = 14.61$ ,  $P = 0.001$ ,  $n = 22$ ). When we excluded the most extreme values (clutches of  $> 30$  eggs), as they could drive the slope to be significant, the analysis still



**Figure 4.** Hatching failures as a result of eggs with incomplete embryo development (closed circles; bold line), bacterial contamination (open circles; dotted line) and being undeveloped (crosses; dashed line) as a function of clutch size.

showed an increase of length of the nesting period with clutch size (regression ANOVA,  $F_{1,19} = 4.92$ ,  $P = 0.04$ ,  $n = 21$ ). Egg temperature at the centre of the nest during incubation tended to decrease with clutch size, but not significantly (regression ANOVA,  $F_{1,7} = 2.02$ ,  $P = 0.19$ ). The variance in egg temperatures during incubation did not vary with clutch size (regression ANOVA,  $F_{1,7} = 0.66$ ,  $P = 0.44$ ). Finally, the frequency of the male's absences from the nest and the length of these absences did not vary with clutch size (regression ANOVA,  $F_{1,7} = 1.29$ ,  $P = 0.30$ , and  $F_{1,7} = 0.17$ ,  $P = 0.69$ , respectively).

Approximately 60% of the chicks reached 40–50 days of age. Chick survival did not vary with brood size after controlling for age (multiple regression ANOVA,  $t = 0.01$ ,  $df = 5$ ,  $P = 0.59$ ).

### Frequencies of clutch sizes

There was no association between the frequencies of clutch sizes and mean hatching success (product moment Pearson correlation,  $r = 0.38$ ,  $Z = 1.46$ ,  $n = 16$ ,  $P = 0.14$ ). The mean number of chicks hatched tended to increase with the frequency of clutch size, although this relationship was not significant (product moment Pearson correlation,  $r = 0.45$ ,  $Z = 1.98$ ,  $n = 16$ ,  $P = 0.08$ ).

### Experimental egg addition

All experimental eggs placed 1.5 m from the border of the nest ( $n = 16$ ) were rolled into the nest by the

incubating male. Hatching success in these experimental nests did not differ from that observed during the same breeding season in nests without manipulation (Fisher exact test,  $P = 0.41$ ). Nests with the experimentally added egg had similar egg losses (Mann–Whitney test,  $Z = 0.04$ ,  $n = 25$  and  $n = 16$ ,  $P = 0.96$ ) and numbers of chicks hatched (Mann–Whitney test,  $Z = 0.60$ ,  $n = 25$  and  $n = 16$ ,  $P = 0.65$ ) to nests where we did not perform any manipulation. In only one case was the experimentally added egg broken during the incubation, but in this nest most of the eggs (23/29) exploded due to bacterial contamination.

## DISCUSSION

The main effect of large communal clutches in Greater Rheas was to reduce hatching success (see also Fernández & Reboreda 1998). Hatching failures are relatively common in birds, with approximately 10% of eggs not hatching (Koenig 1982). In addition, species with complex social systems appear to have a lower hatching success (Koenig 1982). In Greater Rheas, between 20 and 30% of eggs did not hatch. Koenig (1982) suggested the following as factors responsible for such lower hatching success in species with complex social systems: (1) high mating competition that may result in high interference and infertility; (2) high asynchrony among sexes that may result in reduced, delayed or incompetent incubation; and (3) inbreeding. In Greater Rheas, large clutches were the result of large harems (see Fernández & Reboreda 1998), where competition among females could result in interference and higher rates of infertility. However, we failed to find any relationship between clutch size and number of eggs that did not hatch as a result of lack of embryo development (probably infertile eggs).

Large clutches had longer laying and incubation periods (Fernández & Reboreda 1998, this study). Similar results have also been observed in other precocial birds (e.g. Arnold *et al.* 1987, Wallander & Andersson 2002). An increase in the length of incubation may be the result of parents being unable to cover the entire clutch adequately. This could result in greater hatching asynchrony and hatching failures if eggs were exposed more to adverse environmental conditions (Arnold *et al.* 1987, Arnold 1993). In agreement with this interpretation, we found that large clutches had a higher proportion of infected eggs, and a higher number of eggs with incomplete embryo development or with the embryo almost

totally developed (with all yolk sac reabsorbed) but that failed to hatch.

Prolonged laying and incubation also imply an increase in the time eggs are exposed to predators (Clark & Wilson 1981, Ricklefs 1993). Larger clutches in Greater Rheas suffered a higher number of egg losses than smaller clutches. The increase in the length of the nesting period also implies a higher risk of predation for the incubating male in areas where natural predators such as Cougars *Felis concolor* and Jaguars *Oncifelis onca* persist.

Another consequence of prolonged incubation and inadequate conditions for embryo development is the reduced quality of chicks. At suboptimal incubation temperatures, embryos have higher energetic costs of development owing to greater metabolic rates and prolonged incubation (Booth 1987). As a consequence, embryo mortality is higher (Reid *et al.* 2000) and chicks could have lower survival due to depletion of energy reserves and dehydration at hatching (Monaghan & Nager 1997). We found that large clutches tended to have a lower incubation temperature than small clutches. This difference in temperature could explain the higher proportion of hatching failures in large clutches. As mentioned above, we found a higher number of eggs with incomplete embryo development in large clutches, and an increase of embryo mortality. However, we did not find differences in the survival of the chicks (at least during the first 2 months after hatching) between nests differing in clutch size. However, as we did not mark the animals, we cannot rule out differences in long-term survival between chicks hatched from clutches that differ in size.

## Costs of large communal clutches and mating system in Greater Rheas

Although in Greater Rheas hatching failures could be a weaker selective pressure than nest predation or nest desertion, it would nevertheless be an important factor that might influence the evolution of gender reproductive strategies. Hatching failures penalize females that join large harems and therefore lay eggs in large clutches. From an evolutionary point of view, communal laying in a large clutch could be seen as 'the best of a bad job' (i.e. the result of a compromise between not reproducing at all and losing fitness by joining an already mated male). However, the best strategy of a female in a large harem should be to reduce the investment in one particular nest, and search for new opportunities for mating. In

previous studies we suggested that polyandry in Greater Rheas would be constrained by the number of males that attempt to breed in a season (Fernández & Reboresda 1998, 2003). In this scenario, the only possibility for females is to join a large harem. An alternative explanation for large clutches in Greater Rheas is that males with large harems are males of higher genetic or parental quality. If this were the case, we would expect these males to have higher hatching success or chick survival. However, we did not find any supporting evidence for this prediction.

Greater Rhea males are also penalized for accepting large clutches. Although an increase in the number of females generally results in an increase in male fitness (e.g. Ligon 1999), we found that in Greater Rheas there are costs that reduce the benefits of extensive polygyny. We found that large clutches have longer nesting periods. This implies an increased energetic investment by the male, and an increased exposure to predators. These costs, together with those due to egg losses and hatching failures, should impose a limit to the extent of polygyny, or at least should impose a limit to the clutch size a male is willing to incubate. However, we failed to find evidence of male behavioural regulation of clutch size. Furthermore, in a previous work (Fernández & Reboresda 1998) we found that in 17 of 65 nests where we could date exactly the laying day of the eggs, at least one egg was laid at an advanced stage of the incubation (15 days after the laying of the first egg). These eggs were always accepted but they never hatched, although they showed embryonic development at the end of incubation.

Males could use other mechanisms to regulate the size of the clutch, such as a higher level of aggression towards laying females as egg incubation progresses. Bruning (1974) described such behaviour, as well as a reduced tendency to retrieve eggs laid at increased distance from the nest as egg-laying advanced. These behaviours could be seen as an evolutionary response for regulating clutch size.

In summary, large communal clutches provide no benefits for both male and female Greater Rheas. Physiological restrictions that determine egg-laying rates in females, together with mating opportunities and costs for males and females, may have a major role in determining individual success and the extent of polygyny–polyandry in this species. We conclude that different mechanisms involving incubation inability, nest predation risk, mating opportunities and constraints in egg production could contribute to the patterns of communal clutch size observed.

Small clutches require less time for laying and incubation, minimizing exposure to predators (Clark & Wilson 1981) and reducing hatching failures by hatching asynchrony and delayed incubation (Arnold *et al.* 1987, Arnold 1993). In addition, small clutches allow females more time for new mating attempts. These cost–benefit trade-offs together with opportunities for mating are responsible for the distribution of clutch sizes that we observed in Greater Rheas.

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